Phosphorus fertilization by active dust deposition in a super-humid, temperate environment—Soil phosphorus fractionation and accession processes

Andre Eger,[1] Peter C. Almond,[1] and Leo M. Condron[1]

Received 23 February 2012; revised 9 November 2012; accepted 22 December 2012; published 19 February 2013.

[1] The inventory of soil phosphorus (P) is subject to significant changes over time. The main primary form, bedrock-derived apatite P, becomes progressively lost through leaching, or transformed into more immobile and less plant-accessible, secondary organic and mineral forms. Here we studied the rejuvenating effect of dust deposition on soil P along an active dust flux gradient downwind of a braided river. Along the gradient, we measured soil P fractions to 50 cm depth of six Spodosols and one Inceptisol, supplemented by tree foliage P concentrations. While an increasing dust flux correlates with a twofold increase of foliar P and soil organic P along the gradient, apatite P declines from ~50 to 3 g m^{-2} and total P shows no response. Compared to dust-unaffected Spodosols, depth distribution of total P becomes increasingly uniform and organic P propagates deeper into the soil under dust flux. Further, the effect of topsoil P eluviation attenuates due to higher organic P content and the zone of high apatite P concentrations associated with un-weathered subsoil becomes progressively removed from the upper 50 cm. We interpret these patterns as being consistent with upbuilding pedogenesi and conclude that dust-derived mineral P is assimilated in the organic surface horizon and does not reach the mineral soil. Dust-derived mineral P is temporarily stored in the living biomass and returns to the soil with plant and microbial detritus as organic P, which is subsequently buried by further dust increments. We further conclude that (1) the efficiency of P fertilization of the ecosystem by dust accession is higher than through P advection in dust-unaffected Spodosols and (2) organic P may serve as an important source of labile P in a high-leaching environment.

Citation: Eger, A., P. C. Almond, and L. M. Condron (2013), Phosphorus fertilization by active dust deposition in a super-humid, temperate environment—Soil phosphorus fractionation and accession processes, *Global Biogeochem. Cycles*, *27*, 108–118, doi:10.1002/gbc.20019.

1. Introduction

[2] From soil chrono-sequence studies, it is known that the soil phosphorus (P) inventory is subject to distinct changes over time [e.g., *Crews et al*., 1995; *Eger et al*., 2011; *Harrison et al*., 1994; *Selmants and Hart*, 2010; *Vitousek*, 2004]. These studies largely support the seminal P evolution model by *Walker and Syers* [1976], despite showing some variation in timing. Total P declines rapidly in early stages mainly due to heavy losses of primary, parent material-derived apatite P. However, some apatite P is transformed into chemically less mobile (organic P, non-occluded P) and physically protected P fractions (occluded P). These secondary forms retard leaching losses but also make plant assimilation of P more difficult. For many ecosystems without sufficient replenishment of accessible forms of P, this results in retrogression, a decline stage of ecosystem development. In contrast to climax stage communities, retrogression is characterized by plant communities adapted to lower nutrient availability, most crucially of P, through slower growth, greater leaf longevity, and/or reduced productivity, which is often associated with changes in vegetation communities [*Peltzer et al*., 2010; *Vitousek*, 2004; *Wardle et al*., 2004; *Wardle et al*., 2008]. Natural replenishment of P mainly occurs by supplying additional mineral parent material to the soil. This can be achieved by advection of P through the soil column as a result of erosion allowing the weathering front (B-C horizon boundary) to propagate deeper into the subsurface. In a steady state

All supporting information may be found in the online version of this article.

[1]Faculty of Agriculture and Life Sciences, Department of Soil and Physical Sciences, Lincoln University, Lincoln, Canterbury, New Zealand.

Corresponding author: A. Eger, Faculty of Agriculture and Life Sciences, Department of Soil and Physical Sciences, Lincoln University, PO Box 84, Lincoln, Canterbury, New Zealand. (andre.eger@lincolnuni.ac.nz)

0886-6236/13/10.1002/gbc.20019

scenario, erosion rate is in pace with the rate of weathering front propagation (=soil production). Maximum P rejuvenation is achieved when this rate is slow enough to allow for mineral P to be made accessible for plants by weathering and fast enough to avoid accumulation of P-depleted substrate in the rooting zone [*Porder et al*., 2007]. However, in landscapes where erosion rate is lower than soil production, P supply to the rooting zone will eventually decline as a result of declining weathering and soil production with time [*Yoo and Mudd*, 2008a, 2008b]. In such conditions, mineral dust can become an essential rejuvenator for the soil P pool on a global scale. This has been shown for Hawaii, where long-distance atmospheric P contribution from Asia accounts for 90% of the soil P content on 4000 kyr old land surfaces at a deposition rate of 0.25–0.5 g m^{-2} yr^{-1} [*Chadwick et al*., 1999]. *Okin et al*. [2004] expanded earlier work by *Swap et al*. [1992] and analyzed P turnover times in the Amazon Basin and concluded that P sourced from African and Eurasian dust is major control of soil P content of old tropical land surfaces and important in maintaining long-term ecosystem productivity. Thus, changes in global atmospheric circulation and climate conditions affecting dust activity [*Mahowald et al*., 2006] have significant consequences for the global exchange of P. Additionally, by supplying P directly to the soil surface, the part of the soil with the highest biological activity, this may result in different rejuvenation mechanisms than compared to advection from the base of the soil profile. Despite numerous studies on P deposition rates [for an overview, see *Pett-Ridge*, 2009] and specifically throughfall measurements in forests [e.g., *Campo et al*., 2001; *Das et al*., 2011; *Dezzeo and Chacón*, 2006; *Heartsill-Scalley et al*., 2007; *Kellman et al*., 1982; *Newman*, 1995; *Potter et al*., 1991; *Tóbon et al*., 2004], the impact of atmospheric deposition on soil P fractionation is not well known.

[3] To our knowledge, only *Crews et al*. [1995] indicate a potential effect of dust deposition on P fractionation in soils across a 4000 kyr chrono-sequence in Hawaii, where Fe/Al-rich, basalt-derived soils (Andisols, Oxisols) form. They attribute the long-term persistence of high amounts of non-occluded, Fe/Al-associated P to the accession of dust from Asia. For temperate environments with similar super-humid conditions as in Hawaii, we expect different results from the deposition of dust as topsoils are more depleted in Fe/Al oxides due to strong podsolisation and leaching losses in the rooting zone [*Eger et al*., 2011], with potentially long-term effects on P supply. Owing to the varying availability of different P fractions, pedogenic and biological influences on assimilation of dust-derived P into different forms is likely to be important for ecosystem nutrition [e.g., see *Peltzer et al*., 2010].

[4] This paper examines the effect of dust deposition on P fractionation in a temperate environment of rapid pedogenesis along a Holocene dust flux gradient. We quantify how the interplay of pedogenesis and dust flux affects the chemical transformation of selected P fractions (total, organic, apatite, non-occluded, and occluded P). The changes of P fractionation along the dust gradient can be directly related to temporal changes across a nearby chrono-sequence outside the zone of dust additions [*Eger et al*., 2011]. By studying this chrono-sequence, *Eger et al*. [2011] showed that the P evolution model by *Walker and Syers* [1976] was generally applicable to the study area. We will elucidate if dust deposition can act as a backward trajectory in time for the evolution of the soil P inventory (i.e., rejuvenating soil P chemistry by supplying increasing amounts of dust-derived apatite P to the soil).

2. Materials and Methods

2.1. Study Area and Pedogenesis

[5] The study area lies within a foredune barrier system of NE- to SW-aligned shore-parallel coastal sand dunes (beach ridges) on the prograding coastal plain west of the Southern Alps, northwest of the Haast Township, West Coast, New Zealand (Figure 1). Alluvial fans confine the northern and southern ends of the dune complex with occasional outcrops of glacially sculptured quartzofeldspathic metamorphics of the Greenland Group (Late Cambrian-Ordovician). The dune ridges run perpendicular to the braided river bed of the Haast River southwest of the dune system. The drainage basin of the Haast River comprises mainly Permian-Triassic schist of varying degree of metamorphism as part of the Torlesse Terrane from west of the main divide of the Southern Alps [*Rattenbury et al*., 2010]. The sediment transported by the Haast supplies the majority of the material for dune building [*Coates and Nathan*, 1993; *Goff et al*., 2003], and at least for the younger dunes (<1000 years), it has been suggested that dune build-up is associated with episodic sediment pulses brought down the Haast River after earthquakes along the range-bounding Alpine Fault [*Wells and Goff*, 2006, 2007]. The dune complex contains two gradients: a chrono-sequence of dune ridges of increasing age with increasing distance from the coast (~170–6500 years B.P.) [*Eger et al*., 2011; *Wells and Goff*, 2006, 2007] and a dust flux gradient originating from the braided river bed of the Haast with a maximum dust deposition rate of 28.4 g m^{-2} yr^{-1} at the site closest to the river declining with river distance [*Eger et al*., 2012].

[6] This study is set on the oldest, 6500 year old dune, because it is the dune ridge that has been exposed to Holocene dust deposition for the longest time. It therefore has accumulated the highest amount of dust proximate to the river and features the most progressed soil development in soils unaffected by the dust deposition. The differences in soil P inventory between sites under the assumed rejuvenating effect of the dust and soils beyond the no dust influence should be the greatest on this dune. The particular dune is covered by podocarp-angiosperm temperate rainforest. Seven soil pits, labeled H1 through to H7, were dug along the 6500 year old dune on the ridge crest to capture the dust gradient. Soil sites are identical with H1 to H7 in *Eger et al*. [2012]. Distances from the river for each site, measured in a line perpendicular to the NE river bank in a downwind direction, are H1—120 m, H2—220 m, H3—580 m, H4—930 m, H5—1200 m, H6—1790 m, and H7—2620 m. Obvious disturbances like tree overturn and colluvial burial were carefully avoided during soil pit selection. Sites were selected adhering to the following principles for reasons of comparability: preference of flat ridge crests to minimize influence of erosion, avoidance of recent windfall disturbances, and avoidance of dune ridge sections of diminutive size (i.e., <10 m above swales).

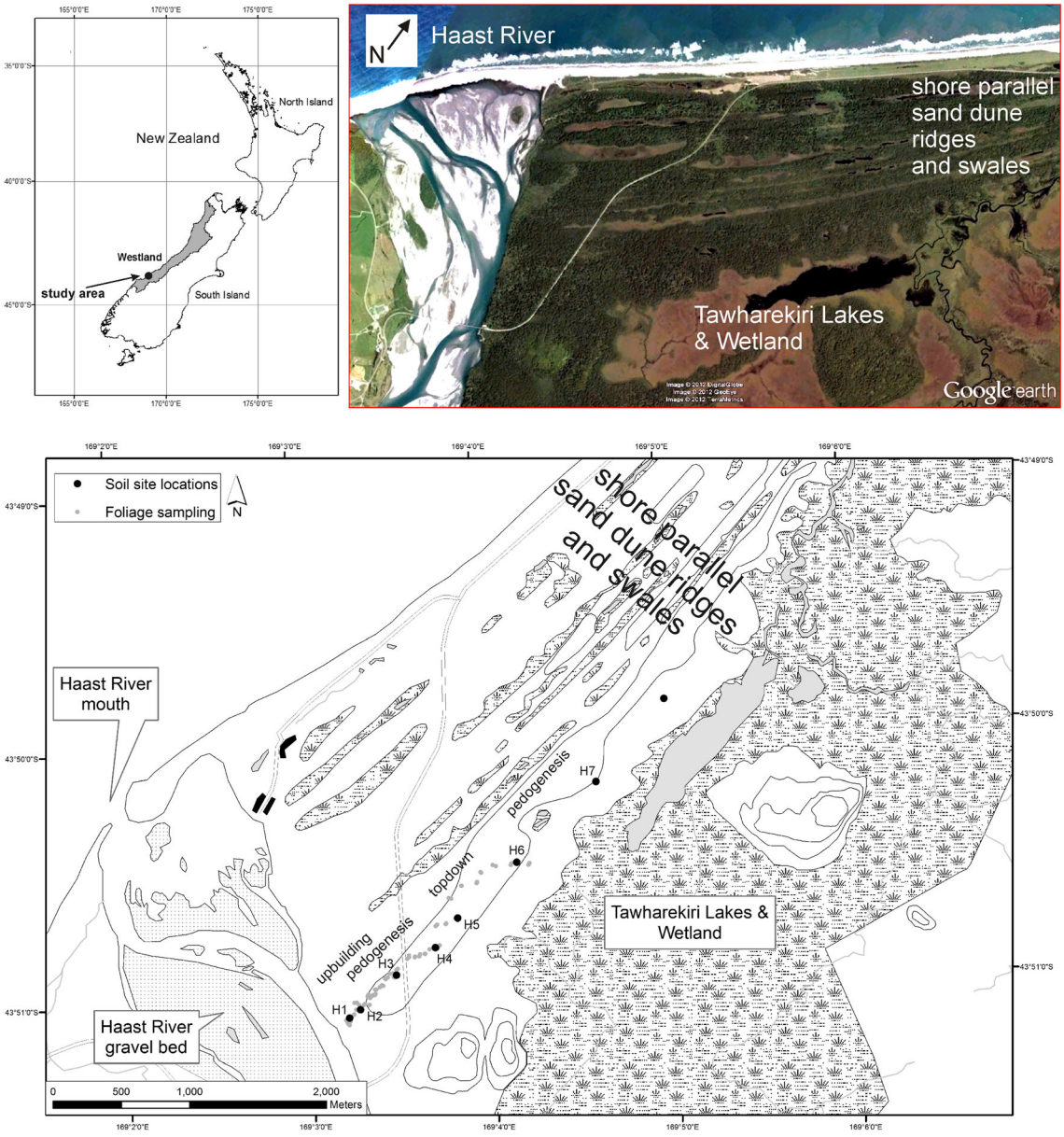

Figure 1. Study area of shore-parallel dune ridges north of the Haast River, West Coast, New Zealand: Soil site locations showing upbuilding and top-down pedogenesis and foliage sampling sites on the 6500 year old dune downwind of the Haast River (satellite image © Google 2012, Image Globe 2012, GeoEye 2012, TerraMetrics 2012).

[7] In accordance with *Eger et al.* [2012], the soils affected by the dust gradient are referred to as upbuilding soils (H1, H2, H3, H4), whereas the sites outside the local dust gradient (H5, H6, H7) as top-down soils. Top-down soils are characterized by an advancing soil formation (weathering) front from the top that causes deepening of the soil with time. In contrast, upbuilding soils are subject to deposition of allochthonous material (e.g., fluvial, aeolian), which is assimilated by the soil formation processes (i.e., pedogenesis is in pace with external deposition). Deepening of the soil mainly occurs in the depositing material, whereas the in situ parent material becomes increasingly disconnected from pedogenic processes [*Almond and Tonkin*, 1999; *Johnson and Watson-Stegner*, 1987]. Soils are Spodosol varieties grading to Inceptisols (H1) under the highest dust flux rate closest to the river. Main pedogenic processes are the translocation of Fe and Al oxides as part of organic chelate complexes from eluvial topsoils to illuvial subsoils, while weathering and leaching losses of soil nutrients are high [*Eger et al.*, 2011]. Upbuilding soils in the study area are formed through burial by continuous dust deposition and concomitant podsolisation such that each dust increment went through the pedogenic stage of the overlying horizons. The substrate of an upwardly growing illuvial B horizon has spent time as an eluvial E horizon and before that as an A horizon. This is controlled by its distance to the surface as the exposure to atmosphere and biota creates the most active weathering environment in the top part of the soil [*Almond and Tonkin*, 1999]. All soils feature distinct eluvial (E) and illuvial (Bs, Bhs, Bh, Bm) horizons, except for H1 where the

Table 1. Profile Totals of P Fractions

	P_{tot}		P_{org}	P_{Ca}	$P_{Fe/Al}$	P_{occ}
	($g\,m^{-2}$)					
Site	0–50 cm	0–30 cm	0–50 cm	0–50 cm	0–50 cm	0–50 cm
H1—120 m	164.64	94.83	91.01	3.10	18.93	51.60
H2—220 m	155.05	76.25	88.07	15.83	16.21	34.94
H3—580 m	152.63	73.16	70.74	14.86	12.65	54.38
H4—930 m	185.88	90.27	72.92	21.79	29.30	61.86
H5—1200 m	156.13	57.76	49.98	42.02	32.70	31.44
H6—1790 m	220.22	59.66	32.13	75.65	36.58	75.86
H7—2620 m	151.20	50.40	47.12	32.28	25.91	45.89

E horizon is replaced by a transitional AE and a Bw horizon. Dust influence, as approximated by soil silt content, increases toward the river in the order of H3, H2, and H1. The upbuilding soils show an increase in thickness of illuvial horizons toward the river with a corresponding increase of secondary Fe/Al-oxides in illuvial horizons and less severe depletion of Fe/Al in the eluvial horizons. Soil organic carbon (SOC) also increases in these soils toward the river, which is especially pronounced for the subsoil. All soils were covered by a thick root mat (8–24 cm), which, together with the A horizons present in the upbuilding soils, contains the vast majority of roots per unit area. Root abundance below the O horizons of top-down soils is very low, but abundance and depth penetration increases in the subsoils of the upbuilding soils toward the river [*Eger et al*., 2012].

2.2. Sampling and Analysis

[8] Soil profiles were dug to >1 m depth; soil P analysis for this study was conducted to 50 cm depth, which captured the soil horizons of each soil above the minimally altered sandy parent material BC or C horizons [*Eger et al*., 2012]. Soil horizon designation and descriptive properties followed *Schoeneberger et al*. [1998]. Sampling followed an incremental procedure guided by soil horizon boundaries. Subsoil samples were taken with a metal core of a known volume, whereas root and organic matter rich topsoils (O, A horizons) were sampled using a modification of the compliant cavity method by substituting water with dry medium sand. Maximum depth of each individual sample increment was 75 mm. Where necessary, increment sample depths were reduced to avoid violation of soil horizon boundaries. Zero datum of reported soil horizon depths is the top of the first mineral horizon.

[9] Total P was extracted by NaOH fusion in nickel crucibles [*Blakemore et al*., 1987; *Smith and Bain*, 1982], and the extracts analyzed by inductively coupled plasma optical emission spectrometry (ICP-OES). Organic P (P_{org}) was extracted following the ignition method of *Saunders and Williams* [1955]. The modified Hedley sequential fractionation with 0.1 M NaOH and 1 M HCl after *Tiessen and Moir* [1993] yielded the non-occluded, iron and aluminum oxide bound P ($P_{Fe/Al}$) and apatite P (P_{Ca}) fraction. P_{org}, $P_{Fe/Al}$, and P_{Ca} extracts were analyzed by the colorimetric method following *Murphy and Riley* [1962] using Murphy and Riley Reagents A and B. The difference between total P and the sum of P_{org}, P_{Ca}, and $P_{Fe/Al}$ is regarded as the occluded/recalcitrant/residual P (P_{occ}). P data are only reported for the mineral horizons. Profile P totals (Table 1) for each soil to a depth of 30/50 cm were calculated using the P concentrations, sample increment depths, and bulk density data upscaled to an area of 1 m^2.

[10] For the approximation for the P concentration of the mineral dust, we took samples of silt-sized sediment from three locations inside the Haast river bed directly north of the road bridge and analyzed them for P_{tot}, P_{Ca}, and $P_{Fe/Al}$.

[11] Above-ground responses to the variable P flux were quantified by foliar sampling and analysis. Our sampling was done at the end of summer in March 2010 and included two of the three main canopy trees, *Dacrydium cupressinum* (common name: rimu) and *Prumnopitys ferruginea* (miro), by shooting (with a shotgun) sunlit branches in the mid-canopy to upper canopy. We used steel shot number 4 (pellet diameter 3.3 mm) and aimed at branches of a maximum diameter of 2 cm. The dislodged branches were collected from the ground and the foliage removed into airtight plastic bags. Foliage was stored in a fridge then sampled by hand plucking to ensure that only fully developed fresh growth was selected for analysis [*Richardson et al*., 2004]. After drying at 60°C for 48 h, samples were ground to a powder and digested in nitric acid heated initially to 40°C followed by 3 × 120 min at 120°C on a digest block. Extracts were analyzed by ICP-OES for main elements; only phosphorus is reported here. Foliage nutrient concentrations are widely used and accepted as one tool of assessing plant nutrient status and ecosystem fertility [e.g., *Aerts and Chapin III*, 1999; *Koerselman and Meuleman*, 1996; *Reich and Oleksyn*, 2004; *Richardson et al*., 2004; *Tessier and Raynal*, 2003; *Vitousek et al*., 1995].

[12] Acting on the assumption made by *Eger et al*. [2012] on the transport process for dust grains through the acidic organic surface layer (i.e., dust is deposited on the ground surface and filters through the organic O horizon until it reaches the first mineral horizon while undergoing weathering and leaching), we wanted to explore if the time required for this transit process is sufficient to substantially influence the chemistry of dust grains by weathering and leaching. Under the assumption of a steady dust flux and steady state O horizon thickness, the transit time of the dust through the O horizon can be estimated as the depth of the O horizon divided by the velocity of the dust moving through the O horizon. This velocity is the ratio of the dust (mass) flux rate and the mass density of dust in the O horizon (equation (1)):

$$\tau = \frac{d_O \rho_O L_O}{100 \cdot L_{\text{flux}}} \tag{1}$$

where τ is the transit time (y), d_O is the depth of the O horizon (cm), ρ_O the bulk density of the O horizon ($g\,cm^{-3}$), L_O the proportion of dust in the O horizon (%), and L_{flux} the dust deposition rate ($g\,cm^{-2}\,yr^{-1}$). For soil H1, the input values are a dust flux of 28.4 $g\,m^{-2}\,yr^{-1}$, a 16 cm thick O horizon with an average bulk density of 0.12 $g\,cm^{-3}$ [*Eger et al*., 2012] and a measured dust content of 35%. This dust content of the O horizon in H1 (L_O) was estimated by loss on ignition on three replicate samples.

[13] In a second modeling exercise, we compared the efficiencies of the two soil rejuvenation mechanisms—advection of nutrients by an advancing soil weathering front and dust deposition. The initial, pre-pedogenesis P_{tot} content over 30 cm depth was estimated for the dune sand parent material (top-down soils) and the dune sand/dust parent material combination (upbuilding soil). Indicated by the

abrupt increase of P_{Ca} concentrations at ~30 cm profile depth in top-down soils, the upper 30 cm are deemed to represent the part of a 6500 year old top-down soil within the weathering zone having entered the biogeochemical cycle. To calculate the initial dune sand P content, the P concentration and bulk density data of a sand sample from 127–134.5 cm depth of H1 were used (see supporting information). For the dust-sand scenario, the total dust accumulation over 6500 years was calculated by using the dust deposition rate of 28.4 g m^{-2} yr^{-1} of H1 [*Eger et al*., 2012] and an assumed bulk density of dust after deposition of 1 g cm^{-3} [*Almond and Tonkin*, 1999]. This equals a thickness of 18.2 cm after 6500 years, which was combined with 11.8 cm of dune sand. The amount of P_{tot} in the dust was calculated using the P_{tot} concentration of the river silts.

3. Results

[14] The soil and foliar P inventory responds to the dust gradient by several major trends that we did not expect; in particular, adding minimally weathered mineral dust to soils under temperate rainforest increases the proportion of the organic P pool in soils while inorganic P declines. The relevant P fraction data are shown in Figure 2, Table 1, and supporting information. Along the gradient, total profile contents of P_{tot} do not change in response to dust flux, whereas P_{Ca} decreases and P_{org} increases with increasing dust deposition in the upbuilding soils. The profile depth distribution in top-down soils shows low concentrations of P_{tot} in the upper ~30 cm of the soil, almost entirely containing P_{org}, P_{occ}, and to a lesser extent $P_{Fe/Al}$, below which an abrupt increase of P_{Ca} occurs. The depth profile of P_{tot} under higher dust flux in upbuilding soils is much more uniform and is increasingly dominated by P_{org} to greater depths at the expense of P_{Ca} with increasing dust flux.

[15] Soil horizons above ~30 cm depth in upbuilding soils show generally higher P_{tot} concentrations than corresponding horizons in top-down soils due to higher abundance of secondary P forms in the upbuilding soils. The opposite is true for the 30–50 cm soil increments, where P_{Ca} in top-down soils (H5, H7: 150–200 μg g^{-1}, H6: 300 μg g^{-1}) exceeds the P_{Ca} concentrations of upbuilding soils. The upbuilding soils feature P_{Ca} concentrations below 10 μg g^{-1} in soil increments above 33 cm (H3), 37.5 cm (H2) and 41.5 cm (H1). Only in the BC horizon of H4 do concentrations of P_{Ca} reach $>$100 μg g^{-1}.

[16] In regard to P_{org}, the depth increment from ~25 to 50 cm in top-down soils is strongly dominated by inorganic P forms with P_{org} concentrations not exceeding 100 μg g^{-1} in B, BC, and C horizons, except for Bh/Bhs horizons. In B horizons of the upbuilding soils H4 and H3, concentrations increase to 100–150 μg g^{-1}. Higher values (180 to 220 μg g^{-1}) in H1 and H2 are maintained to a depth of 37.5 cm (H2) and 41.5 cm (H1). H1 and H2 are the only sites where P_{org} is the most abundant P form in all sample increments of the upper 50 cm. Soil P_{org} content declines systematically with increasing distance from the river following a negative logarithmic regression model ($R^2 = 0.82$, $p < 0.0052$).

[17] Root abundance increases toward the river in both rooting density and depth propagation [*Eger et al*., 2012]. Whereas root abundance in soils H5 to H7 is classified as few and very few, H4 to H1 feature increasing root abundances: common abundance in the A horizon of H4, and many roots in A horizons and greater depth penetration of common root abundances in soils H3 through to H1. E horizons generally have low root abundance (Figure 2). Root abundance, P_{org} concentrations, and organic carbon content [*Eger et al*., 2012] show similar depth relationships along the gradient: relative and absolute increase toward the river and deeper penetration into the subsoil.

[18] The results of the P fractionation of the three samples of river silt (averages) were P_{tot} 1114 μg g^{-1} (1SEM: 34 μg g^{-1}), P_{Ca} 1075 μg g^{-1} (17 μg g^{-1}), and $P_{Fe/Al}$ 32 μg g^{-1} (0.2 μg g^{-1}). This is in accordance to the Munsel color of the samples (5Y 5/1) that indicate that there has occurred only minimal chemical alteration and P is mainly present as primary, mineral P_{Ca} [*Walker and Syers*, 1976].

[19] Foliar P concentrations along the dust gradient are positively correlated with dust flux. Foliar P concentrations strongly decrease over the first 1000 m from the river following a negative logarithmic regression model with distance for both species, *D. cupressinum* ($R^2 = 0.23$, $p < 0.003$, $df = 37$) and *P. ferruginea* ($R^2 = 0.61$, $p < 0.001$, $df = 34$) (Figure 3a).

[20] A similar increase as described for P_{org} concentrations toward the river applies to the foliar P concentrations. Figure 3b shows these relationships clearly for foliar P concentrations and P_{org} content (g m^{-2} 50 cm^{-1}) of the seven soil pits plotted against distance from river, after normalizing the individual P datasets against the highest measured value of each data set.

[21] The calculated transit time through the O horizon for dust of soil H1 is 236 years.

[22] In the comparison of the two rejuvenation scenarios, the 30 cm increment of complete dune sand contains 303 g m^{-2} of P_{tot} at the beginning of pedogenesis, whereas the dust/sand combination originally has 322 g m^{-2}. By using the P content of the upper 30 cm of H6 (60 g m^{-2}) for the sand scenario and H1 (95 g m^{-2}) for the dust/sand combination, H6 retains 20% of its initial P and H1 30%.

4. Discussion

4.1. P Transformations Along the Dust Gradient

4.1.1. Depletion of Apatite P Under Dust Deposition

[23] In the top-down soils H5, H6, and H7, a distinct P_{Ca} increase below ~30 cm profile depth corresponds to the less weathered and chemically depleted BC horizons (dune sand). This reflects the boundary of the advancing weathering front after 6500 years, above which most of the P_{Ca} is leached out of the profile or transformed into secondary P forms, in this case mainly P_{org} and P_{occ}. This is consistent with *Walker and Syers* [1976] and with the chrono-sequence study by *Eger et al*. [2011] who use the same 6500 year old dune but a different pedon as their oldest site. Soils of this age should have lost most of their P_{Ca} in favor of P_{org}, P_{occ}, and $P_{Fe/Al}$. With increasing dust flux, beginning with H4, the P_{Ca} increase in the subsoil becomes more subdued and shifted to greater depths, corresponding to a thickening dust layer and leading to an overall P_{Ca} decline toward the river.

[24] The decline is caused by accumulation of P_{Ca}-depleted dust, while the relatively P_{Ca}-rich sand of the subsoil becomes progressively more removed from the upper 50 cm of the soil. As a consequence, with respect to P sources, the

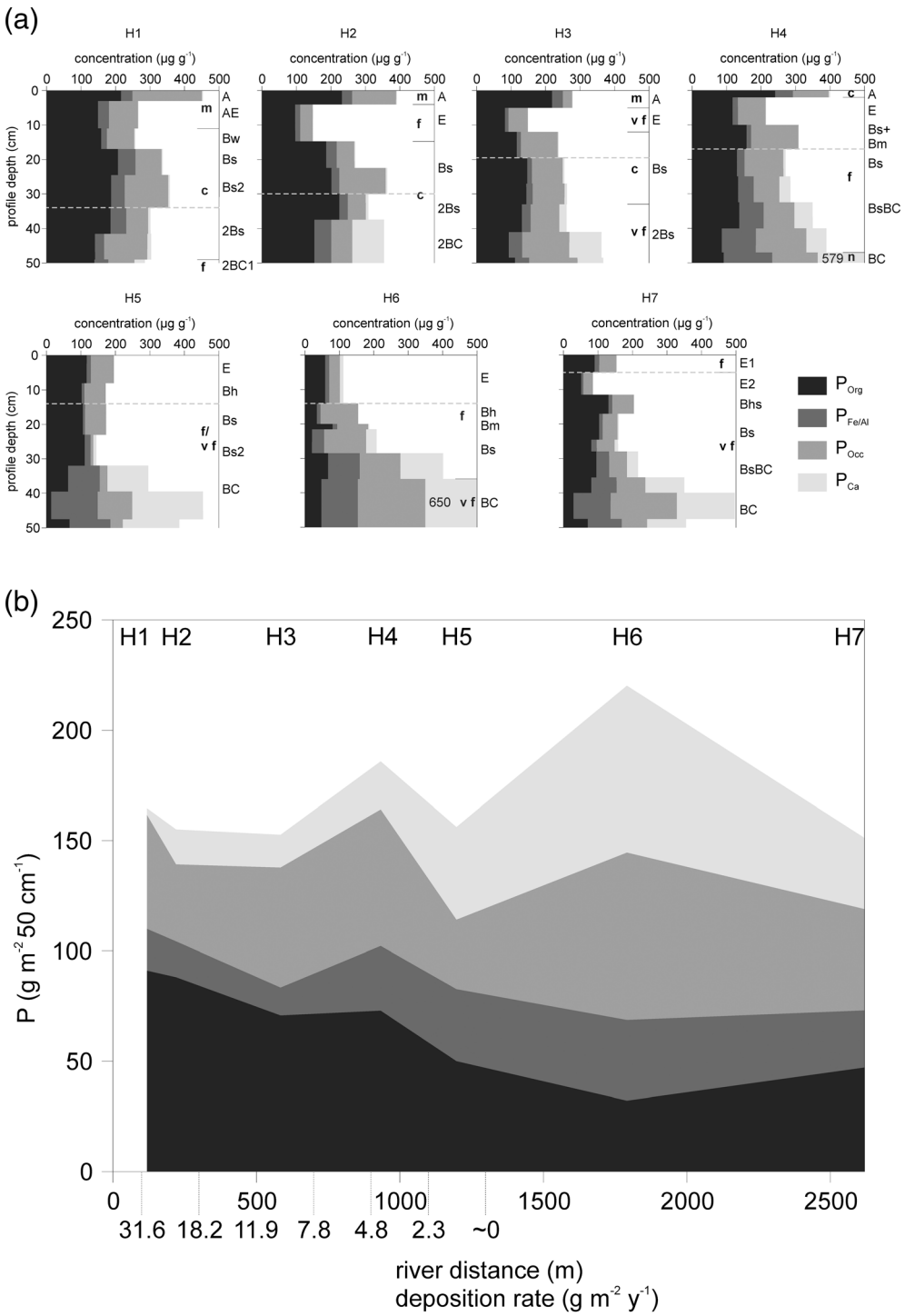

Figure 2. P fractions along the dust gradient: (a) profile depth concentrations for each soil profile; the gray dashed line indicates lower boundary of at least 35% silt content, indicating the changing influence of dust deposition; root abundance for each soil is indicated by tick marks and the abbreviations after *Schoeneberger et al*. [1998]: m—many, c—common, f—few, v f—very few, n—none). (b) soil P profile totals from Table 1; note that the bottom *x* axis has two units, distance from river and dust deposition rate. The dust deposition rate was derived from the regression model [dust deposition $(g\,m^{-2}\,yr^{-1}) = -12.2292 * \ln(x) + 87.9569]$ ($R^2 = 0.90$, $p < 0.001$) depicted in Figure 3a in *Eger et al*. [2012].

upbuilding soil is decoupled from the original, dune sand parent material. The same principle was found by *Almond and Tonkin* [1999] for Pleistocene upbuilding soils, where strongly leached dust buried P_{Ca}-rich coarse-grained glacial till. The majority of P in the incoming dust is in the form of P_{Ca}. During transit through the most reactive, organic surface (O) horizon with the maximum root density, dust becomes depleted in P_{Ca}. It is dissolved in the acidic conditions, and

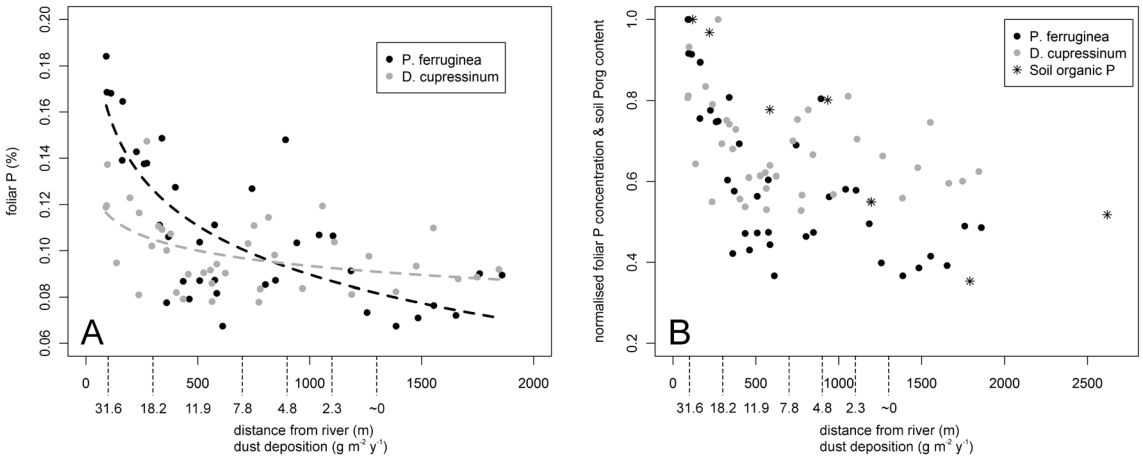

Figure 3. Note that the bottom *x* axes have two units, distance from river and dust deposition rate (for explanation of dust deposition rates, see caption of Figure 2); (a) Change of foliar P concentrations along the dust gradient for *D. cupressinum* and *P. ferruginea*; (b) Plot of foliar P concentrations and soil P_{org} content ($g\,m^{-2}$ 50 cm^{-1})—expressed as normalized values—against distance from river/dust deposition rate.

P_{Ca} is either leached from the soil or assimilated by plants and microorganisms. Instead of supplying P_{Ca} to the mineral soil, the increment of dust emerging at the base of the upwardly migrating O horizon is dominated by secondary P forms, especially P_{org}, and at the same time incorporates organic material of the base of the O horizon. Subsequently, the dust increments depleted of primary P are buried by more recent dust increments and become part of an upwardly thickening spodic Bs horizon [*Almond and Tonkin* 1999; *Eger et al*., 2012].

[25] We also compared the calculated transit time of dust through the O horizon (236 years) with P data from the chrono-sequence study at Haast [*Eger et al*., 2011]. When considering a loss of inorganic P of 86% and H_2SO_4-soluble P (P_{Ca}, $P_{Fe/Al}$) of 90% from the A horizon of the 370 year old soil S_{370} of the Haast chrono-sequence, a Typic Udipsamment [*Eger et al*., 2011], 236 years seems to be sufficient time to deplete the majority of mineral P of the dust, especially given that the O horizon is more acidic (pH 3.9) than the A horizon of S_{370} (pH 4.4) and the dust grains are dispersed in a matrix of organic matter.

4.1.2. Dominance of Secondary P Forms, Particularly Organic P, Under Dust Flux

[26] In contrast to P_{Ca}, P_{org} becomes clearly more dominant with increasing dust flux, both relative and absolute. This especially applies to B horizons in H1 and H2, which are in stark contrast to equivalent horizons in top-down soils. Also, the reduced variability in P_{org} concentration with depth is comparable with the depth pattern of pedogenic oxides in these soils [*Eger et al*., 2012].

[27] We assume that the dust is trapped in the forest canopy and that the majority of the dust reaches the forest floor by canopy drip or stem flow during rain events [*Stoorvogel et al*., 1997]. The mineral dust P is taken up by the forest biota in the O horizon and stored temporarily within the above-ground biomass, estimated to contain ~2.7 $g\,m^{-2}$ of P in West Coast podocarp-hardwood forests [*Levett et al*., 1985]. This assimilation by the vegetation is indicated by the statistically significant response of foliar P of canopy trees to an increasing dust flux. After the death of the organisms, most P is released into the upbuilding soil as P_{org} (biological P cycling) [see *Olander and Vitousek*, 2004; *Condron et al*., 2005] and finally becomes part of the progressively deeper buried dust increments. Rapid transformation of inorganic P into organic P has been observed elsewhere at early stages of soil development [*Egli et al*., 2012].

[28] Potential re-uptake of this subsoil P_{org} by plants ("secondary fertilization") is indicated by the enhanced proliferation of fine roots into B horizons of H1, H2, and H3 (Figure 2) which is probably also linked to the increasing organic matter content [*Koele et al*., 2011]. A greater depth penetration of roots would then cause a positive feedback mechanism of additional subsoil soil carbon (and P_{org}) accumulation and more effective bioturbation to greater depths. Whereas dissolved inorganic phosphate—at early stages of soil development mainly supplied by P_{Ca}—is deemed to be the most plant-accessible form of P in the soil, there are indications that soil P_{org} is more bio-available than previously assumed [*Turner*, 2008]. P_{org} comprises a variety of chemical compounds differing widely in their bioavailability, from weakly sorbed phosphate monoesters to inositol phosphates strongly bound to clays and oxides [*Condron et al*., 2005; *Turner*, 2008]. As a result, the solubilization and hydrolyzation processes that allow plants to utilize P_{org} require a more or less complex range of phosphatase enzymes supported by organic acids and symbiosis with mycorrhizal fungi, and depend on plant species and soil properties [*Johnson et al*., 2003; *Turner et al*., 2007; *Turner*, 2008]. *Johnson et al*. [2003] reviewed soil data on the labile P fraction and observed strong correlation between soil organic matter and labile resin-P concentration, concluding, amongst others that observed a similar relationship [*Hedley et al*., 1982; *Tiessen et al*., 1984; *Tiessen et al*., 1994], that soil organic matter plays a major role in releasing labile forms (e.g., phosphate) of inorganic and organic P. It has been suggested that mineralization of P_{org} and hence its potential release as directly plant-available phosphate by

microbes is limited at early stages of pedogenesis due to low nitrogen availability and slow adaptation to new litter [*Cross and Schlesinger*, 1995]. Neither nitrogen scarcity (indicated by foliar N concentrations along the dust gradient that do not statistically significantly vary (Eger, A. et al., Quantifying ecosystem rejuvenation: foliar nutrient concentrations and vegetation communities across a dust gradient and a chronosequence, submitted to *Plant and Soil*, 2012) nor new litter (surface is 6500 years old) should be factors inhibiting mineralization here; hence, the higher amount of P_{org} should cause an increase in the rate of P mineralization.

[29] Elevated subsoil carbon content and associated P_{org} hence may serve as a long-term source for plant-available nutrients that is less chemically mobile in an acidic environment of rapid depletion of mineral soil nutrients [e.g., *Johnson et al*., 2003] even after the cessation of dust deposition and associated upbuilding pedogenesis (e.g., moving from glacial to interglacial stage [*Mahowald et al*., [2006]).

[30] The importance of the organic surface layer as a place of nutrient uptake for plants/mycorrhizal fungi has been also observed in tropical rainforests, where, according to fertilization studies using radioactively labeled P, 99% of surface applied P does not reach the mineral soil [*Herrera et al*., 1978; *Stark and Jordan*, 1978]. *Pett-Ridge* [2009] also considers the root mat as the part of the soil with the highest nutrient demand best adapted to use ad hoc available nutrients from dust [see also *Jordan and Herrera*, 1981].

[31] Although secondary metal oxides (Fe, Al oxide-hydroxides) of varying crystallinity increase as illuvial horizons thicken as a result of higher dust flux [*Eger et al*., 2012], it is important to note that $P_{Fe/Al}$ and P_{occ} abundances do not increase as one would expect from the literature. P adsorption on pedogenic oxides and later occlusion by these metal oxides, as observed for more progressed pedogenesis (Oxisols, Ultisols) [e.g., *Cross and Schlesinger*, 1995; *Hedley et al*., 1982; *Yang and Post*, 2011], is not promoted by upbuilding pedogenesis. P transformations inferred by *Crews et al*. [1995] for Hawaii are therefore not valid for sites at Haast under a Holocene dust flux. The Hawaiian soils are affected by a dust flux much lower than at Haast [*Chadwick et al*., 1999], whereas SOC abundance is similar or considerably higher than at Haast. Hence, we believe that the absence of rapid upbuilding pedogenesis under environmental conditions favoring podsolisation in Hawaii may explain the differing P assimilation mechanisms under dust deposition between the two sites. The existence of an organic root mat at Haast and the lack of pedogenic oxides in the A and E horizons of upbuilding, podsolized soils at Haast coinciding with a high biological demand for P presumably prevents the formation of adsorbed or occluded inorganic P forms.

[32] The distinct changes in P fractionation along the gradient do not create any clear response of P_{tot} to the dust flux in the upper 50 cm. It seems that the impact of both mechanisms—the P influx by accumulation as P_{org} and the progressive burial of un-weathered dune sand under a thickening dust deposit—counteract each other, regardless of the observed dust deposition rates. Every depth increment of dust adds the same amount of P_{tot} to the soil as is lost through the displacement of a subsoil increment beyond 50 cm soil depth. When focussing on the upper 30 cm only, P_{tot}, however, increases with dust flux due to the higher amount of P_{org} in near-surface soil increments, especially in the A horizons.

[33] We are confident that the interpretation of the observed changes in P fractionation is mainly a response to the dust deposition gradient. Other factors that could potentially explain some of the patterns of P fractionation and other soil properties [*Eger et al*., 2012] are unlikely to be significant here. Flooding from the Haast River does not affect our sites because they are located on top of >10 m high dune ridges that are higher than the broad coastal plain on the opposite (SE) bank of the river. There is no evidence of fluvial deposition from soil profile morphology (e.g., lamination, surface burial) or any signs of fluvial deposition on the forest floor. There are also no indications of the influence of ground water on the studied soils. Possible changes in soil hydrology hence are most likely the result of upbuilding pedogenesis (e.g., deposition of fine-grained dust and absence of drainage-impeding iron pans [*Eger et al*., 2012]). Conventional top-down Spodosols of the study area tend to develop impeded drainage (perch-gleying) as a result of the formation of placic horizons (iron pans) and massive, silty eluvial horizons. This should favor the preservation of organic matter in these Spodosols because of reduced oxidation. However, this study and that of *Eger et al*. [2012] have shown that the upbuilding soils with better drainage properties accumulate more organic matter and organic P because of upbuilding pedogenesis. Vegetation changes were observed along the gradient in form of an increase of species that are typical for young (pre-Spodosol) land surfaces on the west coast of the South Island. However, these changes are restricted to abundances of individual specimens and do not have an effect on plant cover data (e.g., conifer vs. deciduous species), which remain unchanged along the gradient, and hence are not deemed to have sufficient impact on soil P fractions (Eger, A. et al., Quantifying ecosystem rejuvenation: foliar nutrient concentrations and vegetation communities across a dust gradient and a chronosequence, submitted to *Plant and Soil*, 2012).

4.2. P fractions Compared to Soil Chrono-sequence Patterns

[34] That influx of dust does not drive soil rejuvenation equivalent to a backwards arrow of time becomes clear when comparing P along the dust gradient with soil chronosequences used by *Walker and Syers* [1976] to develop the P evolution model and the sequence at Haast [*Eger et al*., 2011]. In regard to mineral P forms only, an increasing dust flux has no rejuvenating effect but instead contributes to a soil that appears to be more leached and chemically altered as it is typical for older soils. In particular, the P_{Ca} decline in the upper 50 cm is much more enhanced than normally found in soils of the same age but unaffected by the local dust input (see also soil S_{6500} by *Eger et al*. [2011]). The dominance of P_{org} to a considerable depth under high dust flux has to be viewed as a distinct feature of upbuilding soils in a high biomass environment and cannot be reconciled with pathways of P assimilation in top-down soils. Figure 4 shows the modified P evolution diagram by *Walker and Syers* [1976] and the differences between the soil P inventory of conventional top-down pedogenesis and upbuilding pedogenesis after 6500 years.

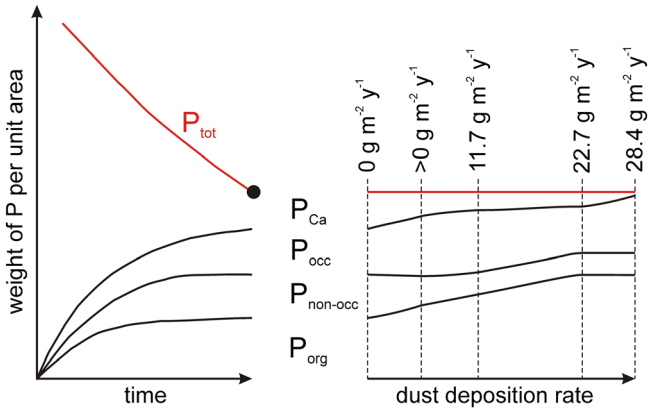

Figure 4. Modified soil P evolution model: Left diagram shows approximate progression of soil P transformation after 6500 years under top-down pedogenesis (black circle), after *Walker and Syers* [1976]; right diagram depicts modification of the soil P inventory by increasing rates of dust deposition over 6500 years, assuming a steady deposition rate.

[35] These contrasts in P fractionation demonstrate the differences between the two soil rejuvenating mechanisms; the input of external substrate onto the soil surface (rejuvenation from the top) on one hand, and advection of parent material by a progressing weathering front (rejuvenation from the bottom) on the other.

[36] The calculations of rejuvenation efficiency by dust deposition versus parent material advection indicate a higher efficiency of rejuvenation by dust deposition than by parent material advection at Haast. Dust-derived P is directly applied to the part of the soils with the highest demand for P, that is, the organic surface layer and topsoil with the highest density of roots. Rapid assimilation leads to an immobilization as P_{org} in the living biomass (e.g., foliage) or plant detritus closer to the root zone, before leaching or inorganic occlusion prevents it from being accessible to the ecosystem. The fact alone that we record an increase of foliar P concentrations toward the river while soil P_{tot} content does not change supports the conclusion that the efficiency of soil P utilization by vegetation is higher in upbuilding soils under dust deposition due to an increase of more plant-accessible P_{org}.

[37] In comparison, P advection from underlying parent material could be less effective, as there is usually a lack of biological activity and fewer roots in the subsoil, despite high amounts of P_{Ca} (e.g., see top-down soils Figure 2). While advecting through the subsoil toward the root zone, P would be constantly subject to predominantly inorganic weathering and leaching processes. By the time an increment reaches the root zone, it is already depleted in P and would also potentially be reduced in plant-available P by occlusion processes. Additionally, the depth advance of the soil formation front declines with soil age if erosion $<$ soil production [*Yoo and Mudd*, 2008a, 2008b], and hence, the advection of parent material will decline. Thus, the fertilizing effect of dust can be regarded as a long-term mitigator of preventing the extreme depletion of soil nutrients and ecosystem retrogression [*Okin et al.*, 2004; *Peltzer et al.*, 2010; *Vitousek*, 2004].

5. Conclusion

[38] This study reveals the importance of biota for the fertilizing effect of dust deposition in a super-humid, temperate climate. The deposition of mineral dust, which supplies P as apatite P, increases soil organic P content and nutrition of main tree species, whereas inorganic P forms, especially apatite P, decline in soils. This requires a process converting dust-derived apatite P to mainly organic forms. We suggest that dust initially filters through the organic surface layer (root mat) of the soil that is highly acidic and promotes intensive chemical weathering with only limited potential for non-organic fixation of P. Rapid assimilation of P by biota in the root mat is followed by its temporary storage in the living biomass. Returned to the soil as organic P as part of plant necromass, the organic material is subsequently buried by successive dust increments and bioturbation. We also suggest a potential secondary fertilization effect by the buried organic matter and associated organic P, which is supported by observations in the literature linking plant-available P forms (labile P) to elevated organic matter content.

[39] This dust accession process supplies mineral P directly to the biologically active part of the soil profile and causes a redistribution of soil P toward the surface and closer to biological demand. This is distinct from the dust-unaffected top-down soils with deep subsoil peaks of apatite P and more strongly P-depleted topsoils.

[40] In top-down soils, which are rejuvenated by advection of parent material-derived P, P-bearing minerals enter the soil from the base due to the advancing weathering front. Advection through the soil column occurs under constant weathering and leaching, which reduces plant-available P before the increment has reached the main rooting zone. Our data support ecosystem rejuvenation by dust being more efficient.

[41] The pathway of P assimilation described for upbuilding soils may be the mechanism by which widespread dust accumulation in the Pleistocene glacials provided a slow-turnover but still plant-accessible soil P pool that mitigates ecosystem retrogression on older land surfaces. Further research should focus on the role of soil organic phosphorus, its plant-accessibility in a dust flux system, and its potential long-term contribution to plant nutrition. Isotope-based methodologies like $\delta^{18}O_P$ seem to be a promising approach [*Paytan and McLaughlin*, 2011].

[42] **Acknowledgments.** This research was financially supported by Brian Mason Trust, Robert Bruce Trust ,and Lincoln University. AE was granted a Lincoln University Doctoral Scholarship. AE gratefully acknowledges Alan Goldin, Charday Wooten-Lane, Judith van Dijk, and Ivan Chirino for invaluable help in the field, Leanne Hassall, Lynn Clucas, and Roger Cresswell for technical support during the laboratory work. The New Zealand Department of Conservation *Te Papa Atawhai* kindly granted permission for working on conservation land.

[43] We thank Eric Sundquist and Aland Townsend in their roles as Editor and Associate Editor. We are very grateful for the thorough comments by two anonymous reviewers, which significantly helped to improve the manuscript.

References

Aerts, R., and F. S. Chapin III (1999), The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns, in *Advances in Ecological Research*, edited by A. H. Fitter and D. G. Raffaelli, pp. 1–67, Academic Press.

Almond, P. C., and P. J. Tonkin (1999), Pedogenesis by upbuilding in an extreme leaching and weathering environment, and slow loess accretion, South Westland, New Zealand, *Geoderma*, *92*(1–2), 1–36.

Blakemore, L. C., B. K. Searle, and B. K. N. Daly (1987), Methods for chemical analysis of soils, *Soil Bureau Scientific Report*, *80*, 103

Campo, J., M. Maass, V. Jaramillo, A. Martínez-Yrízar, and J. Sarukhán (2001), Phosphorus cycling in a Mexican tropical dry forest ecosystem, *Biogeochem.*, *53*(2), 161–179.

Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin (1999), Changing sources of nutrients during four million years of ecosystem development, *Nature*, *397*(6719), 491–497.

Coates, G., and S. Nathan (1993), The Haast Landscape, Institute of Geological & Nuclear Sciences, Lower Hutt.

Condron, L. M., B. L. Turner, and B. J. Cade-Menun (2005), Chemistry and dynamics of soil organic phosphorus, in *Phosphorus Agriculture and the Environment*, edited by J. T. Sims and A. N. Sharpley, pp. 87–121, American Society of Agronomy, Madison.

Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Mueller-Dombois, and P. M. Vitousek (1995), Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii, *Ecol.*, *76*(5), 1407–1424.

Cross, A. F., and W. H. Schlesinger (1995), A literature review and evaluation of the Hedley fractionation: Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems, *Geoderma*, *64*(3–4), 197–214.

Das, R., D. Lawrence, P. D'Odorico, and M. DeLonge (2011), Impact of land use change on atmospheric P inputs in a tropical dry forest, *J. Geophys. Res.*, *116*(G1), G01027.

Dezzeo, N., and N. Chacón (2006), Nutrient fluxes in incident rainfall, throughfall, and stemflow in adjacent primary and secondary forests of the Gran Sabana, southern Venezuela, *Forest Ecol. Manag.*, *234*(1–3), 218–226.

Eger, A., P. C. Almond, and L. M. Condron (2011), Pedogenesis, soil mass balance, phosphorus dynamics and vegetation communities across a Holocene soil chronosequence in a super-humid climate, South Westland, New Zealand, *Geoderma*, *163*(3–4), 185–196.

Eger, A., P. C. Almond, and L. M. Condron (2012), Upbuilding pedogenesis under active loess deposition in a super-humid, temperate climate—Quantification of deposition rates, soil chemistry and pedogenic thresholds, *Geoderma*, *189–190*(0), 491–501.

Egli, M., D. Filip, C. Mavris, B. Fischer, J. Götze, S. Raimondi, and J. Seibert (2012), Rapid transformation of inorganic to organic and plant-available phosphorous in soils of a glacier forefield, *Geoderma*, *189–190*(0), 215–226.

Goff, J. R., S. L. Nichol, and H. L. Rouse (2003), The New Zealand Coast, 312 pp., Dunmore Press, Palmerston North.

Harrison, R., R. S. Swift, and P. J. Tonkin (1994), A study of two soil development sequences located in a montane area of Canterbury, New Zealand, III. Soil phosphorus transformations, *Geoderma*, *61*(3–4), 151–163.

Heartsill-Scalley, T., F. N. Scatena, C. Estrada, W. H. McDowell, and A. E. Lugo (2007), Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico, *J. Hydrol.*, *333*(2–4), 472–485.

Hedley, M. J., J. W. B. Stewart, and B. S. Chauhan (1982), Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations, *Soil Sci. Soc. Am. J.*, *46*(5), 970–976.

Herrera, R., T. Merida, N. Stark, and C. Jordan (1978), Direct phosphorus transfer from leaf litter to roots, *Naturwissenschaften*, *65*, 208–209.

Johnson, A. H., J. Frizano, and D. R. Vann (2003), Biogeochemical implications of labile phosphorus in forest soils determined by the Hedley fractionation procedure, *Oecologia*, *135*(4), 487–499.

Johnson, D. L., and D. Watson-Stegner (1987), Evolution model of pedogenesis, *Soil Sci.*, *143*(5), 349–366.

Jordan, C. F., and R. Herrera (1981), Tropical rain forests: Are nutrients really critical?, *Am. Nat.*, *117*(2), 167–180.

Kellman, M., J. Hudson, and K. Sanmugadas (1982), Temporal variability in atmospheric nutrient influx to a tropical ecosystem, *Biotropica*, *14*(1), 1–9.

Koele, N., F. Storch, and E. E. Hildebrand (2011), The coarse-soil fraction is the main living space of fungal hyphae in the BhBs horizon of a Podzol, *J. Plant Nutr. Soil Sci.*, *174*(5), 750–753.

Koerselman, W., and A. F. M. Meuleman (1996), The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation, *J. Appl. Ecol.*, *33*(6), 1441–1450.

Levett, M. P., A. F. Adams, T. W. Walker, and E. R. L. Wilson (1985), Weight and nutrient content of above-ground biomass and litter of a podocarp-hardwood forest in Westland, New Zealand, *New Zealand Journal of Forestry Science*, *15*(1), 23–35.

Mahowald, N. M., D. R. Muhs, S. Levis, P. J. Rasch, M. Yoshioka, C. S. Zender, and C. Luo (2006), Change in atmospheric mineral aerosols in response to climate: Last glacial period, preindustrial, modern, and doubled carbon dioxide climates, *J. Geophys. Res.*, *111*(D10), D10202.

Murphy, J., and J. P. Riley (1962), A modified single solution method for the determination of phosphate in natural waters, *Anal. Chim. Acta*, *27*, 31–36.

Newman, E. I. (1995), Phosphorus inputs to terrestrial ecosystems, *J. Ecol.*, *83*(4), 713–726.

Okin, G. S., N. Mahowald, O. A. Chadwick, and P. Artaxo (2004), Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems, *Global Biogeochem. Cycles*, *18*, GB2005.

Olander, L. P., and P. M. Vitousek (2004), Biological and geochemical sinks for phosphorus in soil from a wet tropical forest, *Ecosyst.*, *7*(4), 404–419.

Paytan, A., and K. McLaughlin (2011), Tracing the sources and biogeochemical cycling of phosphorus in aquatic systems using isotopes of oxygen in phosphate, in *Handbook of Environmental Isotope Geochemistry*, edited by M. Baskaran, pp. 419–436, Springer, Berlin Heidelberg.

Peltzer, D. A., et al. (2010), Understanding ecosystem retrogression, *Ecol. Monogr.*, *80*(4), 509–529.

Pett-Ridge, J. (2009), Contributions of dust to phosphorus cycling in tropical forests of the Luquillo Mountains, Puerto Rico, *Biogeochem.*, *94*(1), 63–80.

Porder, S., P. Vitousek, O. Chadwick, C. Chamberlain, and G. Hilley (2007), Uplift, erosion, and phosphorus limitation in terrestrial ecosystems, *Ecosyst.*, *10*(1), 159–171.

Potter, C. S., H. L. Ragsdale, and W. T. Swank (1991), Atmospheric deposition and foliar leaching in a regenerating southern Appalachian forest canopy, *J. Ecol.*, *79*(1), 97–115.

Rattenbury, M. S., R. Jongens, and S. C. Cox (2010), Geology of the Haast area. Institute of Geological and Nuclear Sciences 1:250000 Geological Map 14, 58 pp., GNS Science, Lower Hutt.

Reich, P. B., and J. Oleksyn (2004), Global patterns of plant leaf N and P in relation to temperature and latitude, *Proc. Nat. Acad. Sci. U.S.A.*, *101*(30), 11,001–11,006.

Richardson, S., D. Peltzer, R. Allen, M. McGlone, and R. Parfitt (2004), Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence, *Oecologia*, *139*(2), 267–276.

Saunders, W. M. H., and E. G. Williams (1955), Observations on the determination of total organic phosphorus in soils, *J. Soil Sci.*, *6*(2), 254–267.

Schoeneberger, P. J., D. A. Wysocki, E. C. Benham, and W. D. Broderson (1998), Field Book for Describing and Sampling Soils, Natural Resources Conservation Service, USDA, National Soil Survey Center, Lincoln, NE.

Selmants, P. C., and S. C. Hart (2010), Phosphorus and soil development: Does the Walker and Syers model apply to semiarid ecosystems?, *Ecol.*, *91*(2), 474–484.

Smith, B. F. L., and B. C. Bain (1982), A sodium hydroxide fusion method for the determination of total phosphate in soils, *Commun. Soil Sci. Plan.*, *13*(3), 185–190.

Stark, N. M., and C. F. Jordan (1978), Nutrient retention by the root mat of an Amazonian rain forest, *Ecol.*, *59*(3), 434–437.

Stoorvogel, J. J., N. Van Breemen, and B. H. Jassen (1997), The nutrient input by Harmattan dust to a forest ecosystem in Côte d'Ivoire, Africa, *Biogeochem.*, *37*(2), 145–157.

Swap, R., M. Garstang, S. Greco, R. Talbot, and P. Kallberg (1992), Saharan dust in the Amazon Basin, *Tellus B*, *44*(2), 133–149.

Tessier, J. T., and D. J. Raynal (2003), Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation, *J. Appl. Ecol.*, *40*(3), 523–534.

Tiessen, H., and J. O. Moir (1993), Characterization of available P by sequential extraction, in *Soil Sampling and Methods of Analysis*, edited by M. R. Carter and E. G. Gregorich, Canadian Society of Soil Science.

Tiessen, H., J. W. B. Stewart, and C. V. Cole (1984), Pathways of phosphorus transformations in soils of differing pedogenesis, *Soil Sci. Soc. Am. J.*, *48*(4), 853–858.

Tiessen, H., P. Chacon, and E. Cuevas (1994), Phosphorus and nitrogen status in soils and vegetation along a toposequence of dystrophic rainforests on the upper Rio Negro, *Oecologia*, *99*(1/2), 145–150.

Tóbon, C., J. Sevink, and J. M. Verstraten (2004), Solute fluxes in throughfall and stemflow in four forest ecosystems in northwest Amazonia, *Biogeochemistry*, *70*(1), 1–25.

Turner, B. L. (2008), Resource partitioning for soil phosphorus: A hypothesis, *J. Ecol.*, *96*(4), 698–702.

Turner, B. L., L. Condron, S. Richardson, D. Peltzer, and V. Allison (2007), Soil Organic Phosphorus Transformations During Pedogenesis, *Ecosyst.*, *10*(7), 1166–1181.

Vitousek, P. M. (2004), Nutrient Cycling and Limitation, 223 pp., Princeton University Press, Princeton.

Vitousek, P. M., D. R. Turner, and K. Kitayama (1995), Foliar nutrients during long-term soil development in Hawaiian montane rain forest, *Ecol.*, *76*(3), 712–720.

Walker, T. W., and J. K. Syers (1976), The fate of phosphorus during pedogenesis, *Geoderma*, *15*(1), 1–19.

Wardle, D. A., L. R. Walker, and R. D. Bardgett (2004), Ecosystem properties and forest decline in contrasting long-term chronosequences, *Sci.*, *305*(5683), 509–513.

Wardle, D. A., R. D. Bardgett, L. R. Walker, D. A. Peltzer, and A. Lagerström (2008), The response of plant diversity to ecosystem retrogression: Evidence from contrasting long-term chronosequences, *Oikos*, *117*(1), 93–103.

Wells, A., and J. Goff (2006), Coastal dune ridge systems as chronological markers of palaeoseismic activity: A 650-yr record from southwest New Zealand, *The Holocene*, *16*(4), 543–550.

Wells, A., and J. Goff (2007), Coastal dunes in Westland, New Zealand, provide a record of paleoseismic activity on the Alpine fault, *Geol.*, *35*(8), 731–734.

Yang, X., and W. M. Post (2011), Phosphorus transformations as a function of pedogenesis: A synthesis of soil phosphorus data using Hedley fractionation method, *Biogeosci.*, *8*(10), 2907–2916.

Yoo, K., and S. M. Mudd (2008a), Discrepancy between mineral residence time and soil age: Implications for the interpretation of chemical weathering rates, *Geol.*, *36*(1), 35–38.

Yoo, K., and S. M. Mudd (2008b), Toward process-based modeling of geochemical soil formation across diverse landforms: A new mathematical framework, *Geoderma*, *146*(1–2), 248–260.